



Contents lists available at ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/jglr

Spatial and temporal trends in zooplankton assemblages along a nearshore to offshore transect in southeastern Lake Michigan from 2007 to 2012

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ARTICLE INFO

Article history:

Received 2 April 2014

Accepted 8 August 2014

Available online xxxx

Communicated by David Bunnell

Keywords:

Crustacean

Great Lakes

Oligotrophication

Dreissena

Planktivory

ABSTRACT

Zooplankton were collected at a nearshore (15 m depth), a mid-depth (45 m) and an offshore site (110 m) near Muskegon, Michigan during March–December in 2007–2012. On a volumetric basis, biomass was lower at the nearshore site relative to the mid-depth site, but overall biomass at the nearshore and offshore sites did not differ. Differences in zooplankton assemblages among sites were due largely to Diaptomidae, *Limnocalanus macrurus*, *Daphnia galeata mendotae*, *Cyclops*, and either *Bosmina longirostris* or *Bythotrephes longimanus*. Diaptomidae were the most abundant group, accounting for 56–66% of zooplankton biomass across sites. Herbivorous cladocerans accounted for 14–22% of zooplankton biomass across sites, with *B. longirostris* dominant at the nearshore site and *D. g. mendotae* dominant at the mid-depth and offshore sites. *Bythotrephes* was the most abundant predatory cladoceran at all sites although, at the nearshore site, it was only abundant in the fall. There was a higher percentage of large-bodied zooplankton groups in the offshore and mid-depth zones relative to the nearshore zone. Declines in zooplankton biomass relative to the 1970s have occurred across all sites. In addition to seasonal variation within a site, we noted annual variation, especially at the offshore site, with the zooplankton assemblage during 2007–2008 differing from that found in 2010–2012 due to increases in *D. g. mendotae* and *Cyclops* and decreases in *B. longimanus* and *L. macrurus* in 2010–2012.

Published by Elsevier B.V. on behalf of International Association for Great Lakes Research.

Introduction

The offshore food web in Lake Michigan has recently shifted toward a more oligotrophic state (Evans et al., 2011). Changes such as the diminished spring bloom (Fahnenstiel et al., 2010), smaller summer deep chlorophyll layer (Pothoven and Fahnenstiel, 2013), and shifts in zooplankton community structure (Vanderploeg et al., 2012) have been associated with the expansion of dreissenid mussels into the offshore region. However, little is known about the current status of the nearshore zooplankton community, and how it compares with that in the offshore. Most studies of zooplankton in the Great Lakes take place in offshore region even though the nearshore region is an important habitat for fish, especially young fish. However, the offshore region is probably a poor surrogate of ecological conditions in nearshore regions (Hall et al., 2003; Schelske et al., 1980) because the zooplankton communities in nearshore and offshore regions likely respond differently to environmental changes (Evans and Jude,

1986) and biotic (phytoplankton availability, predator abundance) and abiotic (light, temperature) conditions differ between these habitats.

In the 1970s, primary production and chlorophyll levels were higher in nearshore regions than in offshore regions (Bartone and Schelske, 1982; Schelske et al., 1980), but biomass of zooplankton was highest in a mid-depth region at depths of 20–50 m on both an areal and volumetric basis (Evans, 1990; Hawkins and Evans, 1979). Based on very limited data, zooplankton biomass on a volumetric basis was probably less at sites deeper than 50 m than in nearshore habitats (Scavia et al., 1986). Dreissenid mussels sequester nutrients in nearshore zones (Hecky et al., 2004) or in mid-depth regions between the nearshore and offshore regions (Vanderploeg et al., 2010). However, the nutrients sequestered by dreissenids in nearshore regions could be enhancing benthic production of undesirable algae such as *Cladophora* spp. at the expense of pelagic components such as zooplankton (Depew et al., 2006; Hecky et al., 2004; Johannsson et al., 2000). As the offshore habitat becomes more oligotrophic, zooplankton abundance in this region could also decline (Vanderploeg et al., 2012). One consequence of the oligotrophication of the offshore region and the benthification of the nearshore region is that zooplankton biomass in offshore habitats could become more similar to that found in nearshore regions, a scenario that occurred in Lake Ontario (Hall et al., 2003).

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Zooplankton community structure has also differed between nearshore and offshore habitats in Lake Michigan. In general, smaller zooplankton are found in nearshore habitats than in the offshore habitats due to the disproportionate influence of size selective fish predation pressure in nearshore regions (Evans, 1990; Evans et al., 1980; Evans and Jude, 1986). During 2007–2012, planktivorous fish biomass in Lake Michigan declined to record lows in a time series going back to 1973 (Bunnell et al., 2014). This relaxation in fish predation could result in a convergence in zooplankton community structure between the nearshore and offshore regions in the lake. Fish predation can also influence the composition and abundance of predatory cladocerans, including invasive species such as *Bythotrephes longimanus* (Pothoven et al., 2007). *B. longimanus* is generally most abundant in offshore regions where fish predation is low (Cavaletto et al., 2010). In turn, predation by *B. longimanus* can alter zooplankton community structure (Barbiero and Tuchman, 2004; Lehman and Cáceres, 1993; Makarewicz et al., 1995). A relaxation in fish predation might lead to higher densities of *B. longimanus*, especially in nearshore regions, where fish planktivory exceeds *B. longimanus* production (Pothoven et al., 2007). In turn, *B. longimanus* biomass could become more similar between nearshore and offshore regions.

The goal of this study was to evaluate variation in zooplankton assemblages between a nearshore, a mid-depth, and an offshore site in southeastern Lake Michigan during 2007–2012, a period of dynamic changes in the dreissenid mussel populations in the lake. Dreissenid

mussel populations were relatively stable in the nearshore region, but populations were expanding and increasing in the offshore region (S. Pothoven, unpublished data). We expected that in contrast to historical patterns, zooplankton biomass and community structure would now be similar among sites owing to oligotrophication and benthification following mussel invasion and an overall relaxation in fish predation. We also evaluated seasonal and inter-annual variation within each site within this dynamic period. We expected that there would be seasonal and annual trends within each site owing to variation in factors such as thermal conditions or phytoplankton abundance.

Methods

Zooplankton were collected at a nearshore site (15 m depth), a mid-depth site (45 m depth) and an offshore site (110 m depth) near Muskegon, Michigan during 2007–2012 (Fig. 1). Sampling took place at each site 1–2 times each month during March–December each year although in a few cases sampling did not take place during a particular month due to weather constraints.

Zooplankton were collected using duplicate tows of a 50-cm diameter, 2.5-m long, 153- μ m mesh, conical net equipped with a flowmeter. The net was hauled vertically through the water column at a speed of 0.5 m/s from 1–2 m above the bottom to the surface. Zooplankton were narcotized with Alka-Seltzer and preserved in 2–4% sugar formalin solution. In the laboratory, an aliquot was removed using a Hensen-

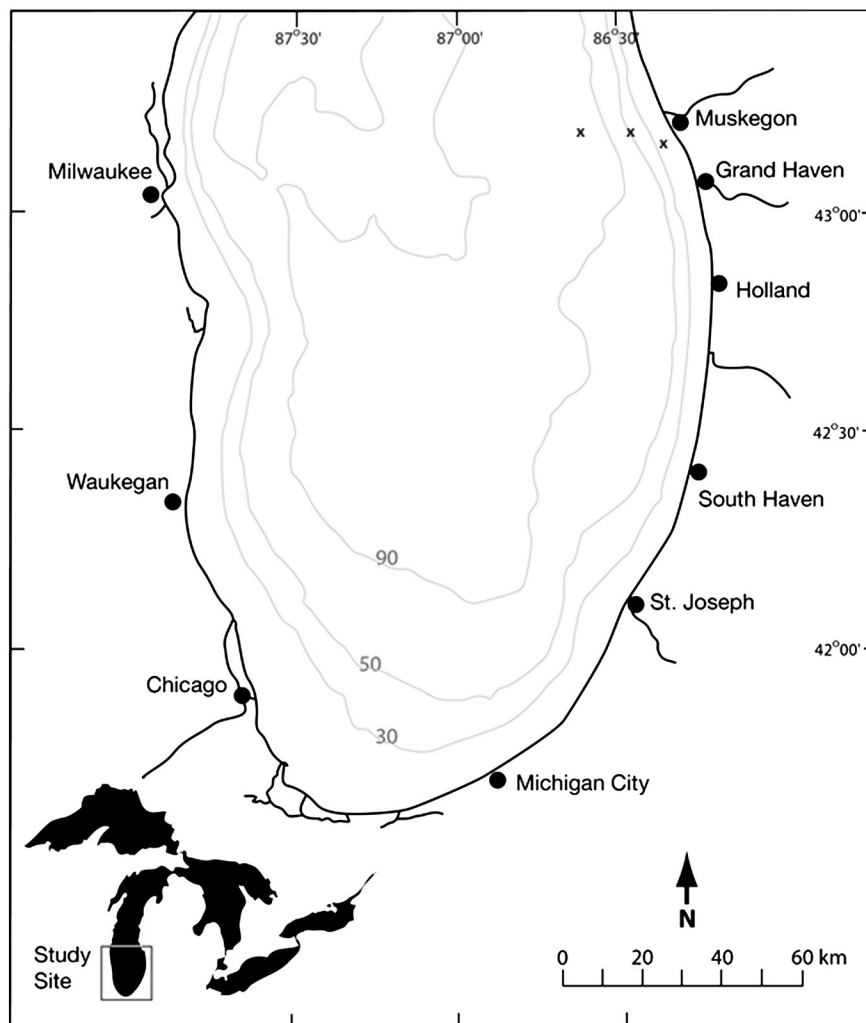


Fig. 1. Map of sampling area showing location (x) of nearshore, mid-depth, and offshore sampling sites.

Stempel pipette so that a minimum of 600 zooplankton were identified for each sample. To count large predatory cladocerans, i.e., *B. longimanus*, *Cercopagis pengoi*, *Leptodora kindtii*, and *Polyphemus pediculus*, the whole sample was rinsed through a 600- μ m mesh sieve and all individuals were counted. Counts from each replicate tow were averaged for each site and date to provide a single estimate of zooplankton abundance.

All cladocerans and adult copepods were identified using the keys of Balcer et al. (1984). To determine zooplankton biomass, length measurements were made using Image Pro Plus on a subsample of taxa (10 adult copepods and 25 copepodites or cladocerans) that were over 10% of the total density. In the case of large predatory cladocerans, all individuals were measured or up to 100 individuals if more than that were present. Biomass was determined using published length-weight regressions (Culver et al., 1985; Makarewicz and Jones, 1990). We recognize that these length-weight regressions underestimate biomass of adult copepods such as *Leptodiptomus sicilis* and *Limnocalanus macrurus* during summer and fall when these species lay down abundant lipid reserves in preparation for reproduction (Vanderploeg et al., 1992, 1998; Doubek and Lehman, 2011). For unmeasured zooplankton taxa that comprised less than 10% of the total density, a default weight from the literature was used to determine biomass (Hawkins and Evans, 1979). Biomass densities were calculated on a volumetric basis.

Some copepod species were combined into two separate groups prior to analysis because copepodites were not differentiated among species, i.e., 1) Diaptomidae (*Leptodiptomus ashlandi*, *L. sicilis*, *L. minutus*, *Skistodiptomus oregonensis*), and 2) Cyclops (*Acanthocyclops vernalis* and *Diacyclops bicuspidatus*). The cladocerans *Chydorus* spp., *Diaphanosoma* spp. and *Ceriodaphnia* spp. were not identified to species and were grouped by their respective genus. For analysis, data were combined into 4 seasons, i.e., spring (March–May), early summer (June–July), late summer (August–September), and fall (October–December). These periods roughly correspond to spring isothermal, early stratification, late stratification, and fall as noted by Fahnenstiel et al. (2010).

Along with each zooplankton collection, water temperature was determined from the surface to just above the bottom and binned into 1-m depth increments using a Seabird CTD (conductivity, temperature, and depth) equipped with a Turner or Wet Labs fluorometer. Discrete samples of water for chlorophyll *a* analysis were taken from 1 to 6 depths in the water column with a modified Niskin bottle (Fahnenstiel et al., 2002) and poured into acid-cleaned polycarbonate carboys (1-carboy for each depth) from which all water samples were taken. Water for chlorophyll *a* analysis was filtered under low vacuum onto Whatman GF/F filters, extracted with N, N-dimethylformamide (Speziale et al., 1984) and analyzed fluorometrically. Fluorometer voltage from the CTD was converted to chlorophyll *a* concentration with regressions developed using extracted concentrations of chlorophyll *a* (see Pothoven and Fahnenstiel, 2013). The surface and average water column temperatures were determined as well as the surface mixed layer and average water column chlorophyll *a* concentrations.

Non-metric multidimensional scaling (MDS) was used to visualize differences in zooplankton community structure in two dimensions with biomass data from each site-date-year as the input. Square root transformed abundance data were used to create a Bray–Curtis similarity matrix as the input for MDS. MDS is an ordination technique that is relatively insensitive to data distributions (i.e., non-normality and non-linearity) compared to other multivariate ordination methods (Clarke and Warwick, 2001).

Analysis of similarities (ANOSIM) was used to test for differences in zooplankton community structure between sites. A two-way ANOSIM was also used to test for differences in community structure among seasons or years within each site. ANOSIM is analogous to an ANOVA with a non-parametric permutation applied to a rank similarity matrix of samples (Clarke and Warwick, 2001). Pairwise R-values from ANOSIM were used as a measure of absolute separation between groups. R-values range from -1 to $+1$, and generally lie between 0 (indistinguishable) and $+1$ (all similarities within groups are less than

any similarity between groups) (Clarke and Gorley, 2001). A similarity percentage routine (SIMPER) was applied to determine overall contribution of each species to dissimilarity between sites or between years and seasons within sites. MDS, ANOSIM, and SIMPER were performed using Primer v5.2.9. A Kruskal–Wallis test was used to compare differences in total zooplankton or *Bythotrephes* biomass among sites followed by non-parametric pairwise tests.

Results

Variation among sites

Overall total zooplankton biomass differed among sites (KW test = 8.0, $p = 0.02$, $df = 2$), due to relatively low biomass at the nearshore site relative to the mid-depth site (Table 1). Overall total biomass at the offshore site did not differ significantly from that at the mid-depth or the nearshore sites ($p > 0.05$). Overall total predatory cladoceran biomass did not differ among sites (KW test = 0.4, $p = 0.8$, $df = 2$), but *B. longimanus* biomass differed between each site (KW test = 7.4, $p = 0.02$, $df = 2$), with highest overall biomass at the offshore site and lowest at the nearshore site (Table 1).

Overall, ANOSIM indicated that the zooplankton assemblages differed among sites ($R = 0.142$, $p < 0.001$), with the least overlap in zooplankton assemblages found between the nearshore and offshore sites ($R = 0.25$) and the most overlap between the offshore and mid-depth sites ($R = 0.07$) (Fig. 2). Within each season, ANOSIM indicated that the zooplankton assemblages differed among sites ($p < 0.002$), but the degree of separation varied by season. In the spring and fall there was still considerable overlap in zooplankton assemblages (Fig. 2). In contrast, in early and late summer, there was more separation in zooplankton assemblages among sites largely because the offshore site, and to a lesser degree the mid-depth site, were well separated from the nearshore site (Fig. 2).

Based on SIMPER analysis, the differences in zooplankton assemblages among sites were due largely to Diaptomidae, *L. macrurus*, *D. g. mendotae*,

Table 1

Mean biomass and percent contribution for each zooplankton group at the nearshore, mid-depth, and offshore site in southeastern Lake Michigan during 2007–2012. Total biomass values that share a common superscript letter were not significantly different among sites (nonparametric multiple comparison test).

	Volume mg/m ³			Percent		
	Near	Mid	Off	Near	Mid	Off
Nauplii	0.39	0.16	0.16	2	1	1
Cyclops	0.98	1.52	1.06	5	6	5
Mesocyclops edax	0.03	0.02	0.01	<1	<1	<1
Tropocyclops prasinus	0.03	0.02	0.01	<1	<1	<1
Diaptomus spp.	11.08	17.00	12.52	56	66	56
Epishura lacustris	0.84	0.64	0.41	4	2	2
Eurytemora affinis	0.04	<0.01	<0.01	<1	<1	<1
Senecella calanoides	0.01	0.03	0.08	<1	<1	<1
Limnocalanus macrurus	0.89	2.04	3.35	4	8	15
Bosmina longirostris	3.3	0.75	0.15	16	3	1
Eubosmina coregoni	0.12	0.03	0.01	1	<1	<1
Ceriodaphnia spp.	0.01	<0.01	0	<1	<1	0
Chydoridae	0.06	<0.01	<0.01	<1	<1	<1
Daphnia galeata mendotae	1.05	2.71	3.56	5	10	18
D. longiremus	<0.01	<0.01	0	<1	<1	<1
D. retrocurva	0.02	<0.01	<0.01	<1	<1	<1
D. pulicaria	0	<0.01	<0.01	<1	0	<1
Diaphanosoma spp.	<0.01	<0.01	<0.01	<1	<1	<1
Bythotrephes longimanus	0.29	0.33	0.50	1	1	2
Cercopagis pengoi	0.07	0.01	<0.01	<1	<1	<1
Leptodora kindtii	0.05	0.04	0.01	<1	<1	<1
Polyphemus pediculus	0.02	<0.01	<0.01	<1	<1	<1
Veliger	0.67	0.30	0.08	3	1	<1
Total	19.97 ^a	25.64 ^b	22.21 ^{ab}			

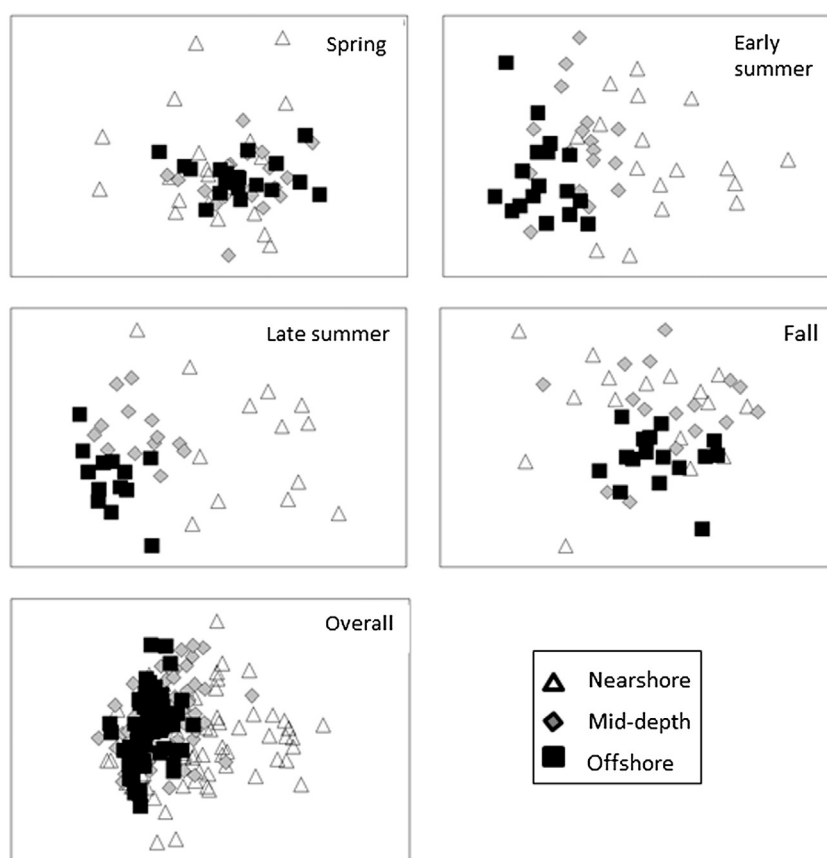


Fig. 2. Multidimensional scaling ordination of three sites in Lake Michigan in spring, early summer, late summer, fall, and overall based on Bray–Curtis similarities of zooplankton community assemblages.

Cyclops, and either *Bosmina longirostris* or *B. longimanus* (Table 2). Overall, calanoid copepods dominated the zooplankton community at each site, accounting for 65% (nearshore), 77% (mid-depth) and 73% (offshore) of all zooplankton biomass (Table 1). Diaptomidae were the most abundant calanoid group, accounting for 56–66% of zooplankton biomass. About 44% (offshore) to 49% (nearshore) of the diaptomid biomass was accounted for by juveniles. *Leptodiaptomus ashlandi* and *L. sicilis* were the most abundant adult diaptomids, with higher proportions of *L. sicilis* at the mid-depth and offshore sites (Fig. 3). The highest proportion of *L. minutus* was at the nearshore site, and *S. oregonensis* were rare at all

sites. After Diaptomidae, the next most abundant calanoid copepod group was *L. macrurus*, which accounted for a higher percentage of the zooplankton biomass offshore (15%) compared to nearshore (4%). *Cyclops*, although important to differentiate sites, accounted for <6% of zooplankton assemblage at each site. Herbivorous cladocerans accounted for 22% (nearshore), 14% (mid-depth), and 18% (offshore) of all zooplankton biomass. The herbivorous cladoceran community was dominated by *B. longirostris* at the nearshore site and by *D. g. mendotae* at the mid-depth and offshore sites. *Bythotrephes* was the most abundant predatory cladoceran at all sites.

Table 2

The percent contribution of the top five zooplankton groups to the dissimilarity between pairs of sites from the SIMPER analysis.

Site	Group	Percent
Nearshore vs mid-depth	Diaptomidae	21
	<i>B. longirostris</i>	12
	<i>L. macrurus</i>	11
	<i>D. galeata mendotae</i>	10
	<i>Cyclops</i>	9
Nearshore vs offshore	Diaptomidae	18
	<i>L. macrurus</i>	14
	<i>B. longimanus</i>	12
	<i>D. galeata mendotae</i>	10
	<i>Cyclops</i>	8
Mid-depth vs offshore	Diaptomidae	16
	<i>D. galeata mendotae</i>	16
	<i>L. macrurus</i>	14
	<i>Cyclops</i>	11
	<i>B. longimanus</i>	7

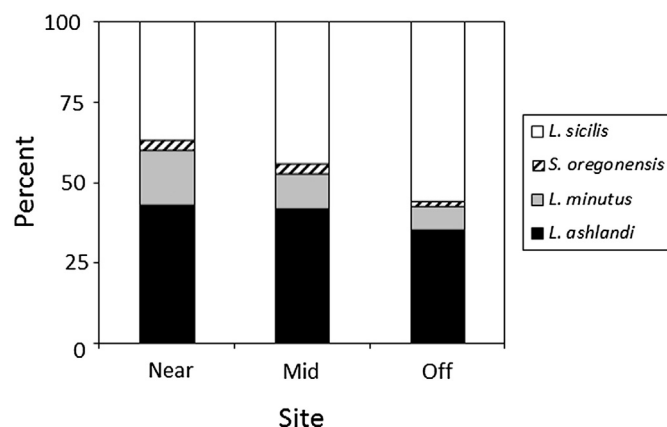


Fig. 3. Species composition (%) of Diaptomidae adults at a nearshore, mid-depth and offshore site in southeastern Lake Michigan during 2007–2012.

Table 3

Environmental characteristics (surface water temperature, average water column temperature, surface mixed layer chlorophyll concentration, average water column chlorophyll concentration) at each site in southeastern Lake Michigan during 2007–2012.

		Surface T	Average T	SML chl	Average chl
		°C	°C	µg/L	µg/L
Nearshore	Spring	6.2	5.5	2.5	2.2
	Early summer	18.0	14.3	2.7	1.9
	Late summer	20.0	16.7	1.8	1.2
	Fall	10.4	10.7	2.0	1.6
	Average	13.1	11.4	2.3	1.8
Mid-depth	Spring	4.3	3.9	0.7	0.8
	Early summer	17.8	9.5	1.6	1.2
	Late summer	21.1	11.0	1.2	0.9
	Fall	11.1	10.1	1.5	1.1
	Average	12.8	8.3	1.2	1.0
Offshore	Spring	3.4	3.3	0.9	1.0
	Early summer	16.8	6.8	0.9	1.1
	Late summer	22.0	7.6	1.0	0.8
	Fall	11.1	7.5	1.8	0.9
	Average	12.5	6.1	1.1	1.0

Overall average water column temperature, surface water temperature, average chlorophyll *a* concentration, and surface mixed layer chlorophyll *a* concentration were highest at the nearshore site and lowest at the offshore site (Table 3).

Seasonal variation within sites

ANOSIM indicated that there were significant differences in the zooplankton assemblage among seasons within each station ($p = 0.001$). However, patterns among seasons differed within sites. At the nearshore site, the most separation in zooplankton assemblages was between the spring and early/late summer, whereas fall was marginally separated from other seasons, and early and late summer were indistinguishable (Fig. 4). SIMPER indicated that the dissimilarity between spring and early/late summer at the nearshore site was largely due to differences in three zooplankton groups, *B. longirostris*, Diaptomidae, and *L. macrurus*. Total biomass at the nearshore site increased from spring into early summer, mainly due to the appearance of the cladoceran *B. longirostris* and an increase in Diaptomidae (Fig. 5). By contrast, *L. macrurus* decreased after spring sampling. Biomass trended downward in the fall, corresponding largely to a decrease in *B. longirostris*. The nearshore zooplankton assemblage was >92% copepods in spring and fall, but

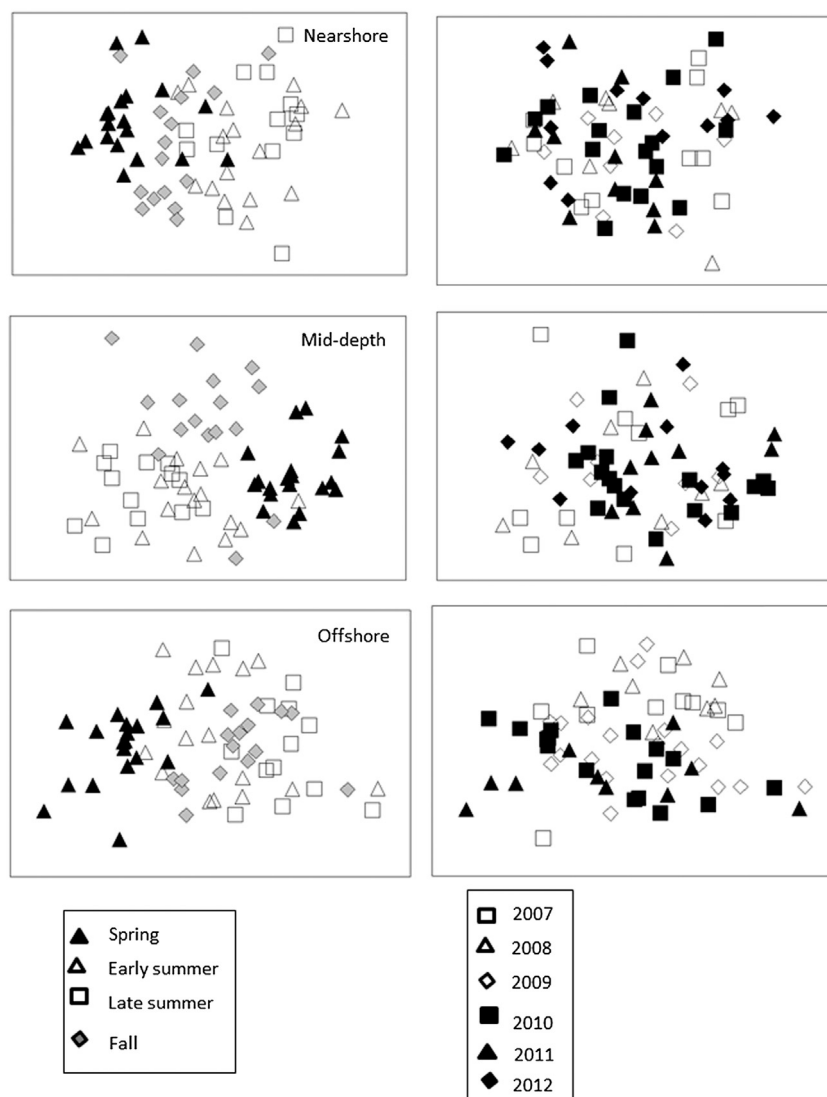


Fig. 4. Multidimensional scaling ordination of seasons (left) and years (right) at three sites in Lake Michigan based on Bray–Curtis similarities of zooplankton community assemblages.

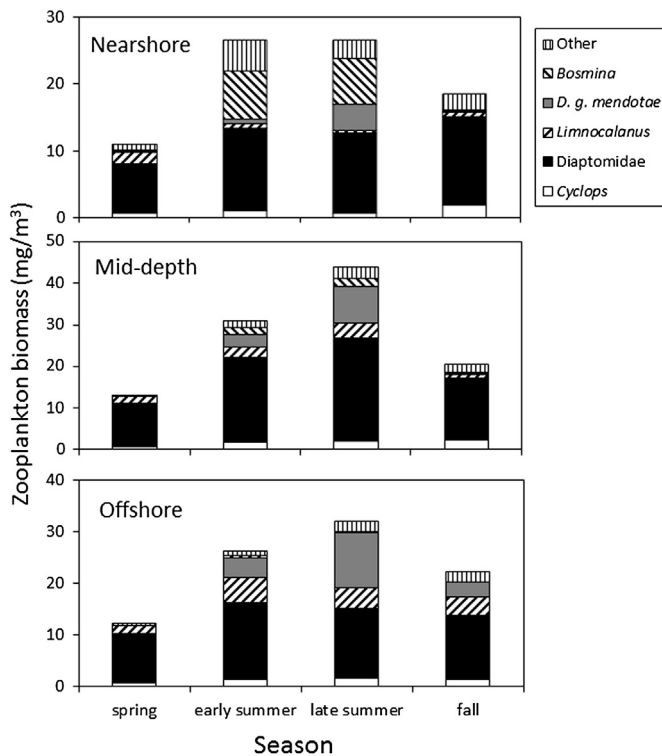


Fig. 5. Mean biomass concentration of zooplankton at a nearshore, mid-depth, and offshore sites in southeastern Lake Michigan during spring, early summer, late summer, and fall for the period 2007–2012.

only 60 and 55% copepods in early and late summer, respectively. The predatory zooplankton biomass peaked in the fall at the nearshore site, when *B. longimanus* were most abundant and accounted for 5% of the total zooplankton biomass (Fig. 6). Total biomass of predatory cladocerans was similar in early and late summer, but the predatory cladoceran

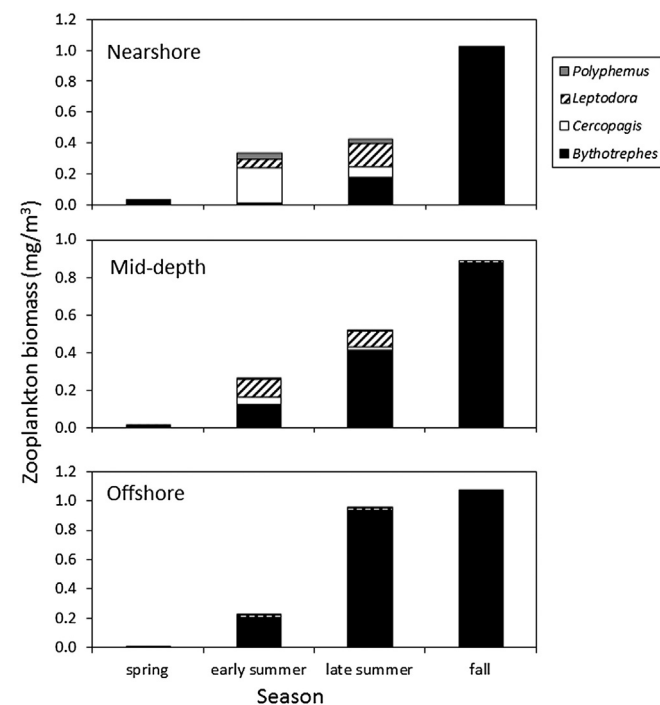


Fig. 6. Mean biomass concentration of predatory cladocerans at a nearshore, mid-depth, and offshore site in southeastern Lake Michigan during spring, early summer, late summer, and fall for the period 2007–2012.

assemblage shifted from one dominated by *C. pengoi* to one dominated by *L. kindtii* and *B. longimanus*.

At the mid-depth site, the most separation among seasons was related to spring being well separated from all other seasons (Fig. 4). SIMPER indicated the dissimilarity between spring and early/late summer was due to a combination of Diaptomidae, *B. longirostris*, *D. g. mendotae*, *L. macrurus*, and *Cyclops* spp., which all increased between spring and summer so that peak overall biomass occurred in late summer (Fig. 5). By contrast, the differences between spring and fall were related to Diaptomidae, *Cyclops* spp., *B. longimanus*, and *E. lacustris*, which all increased between the spring and fall, and to *L. macrurus* which decreased. Diaptomidae, *L. macrurus*, and *D. g. mendotae* all decreased between summer and fall. Copepods accounted for 99–92% of the zooplankton biomass in the spring and fall, respectively, at the mid-depth site, and 82–73% in the early and late summer, respectively (Fig. 5). The biomass of predatory cladocerans increased from early summer into late summer and peaked in the fall, when 4% of the total zooplankton biomass was comprised of predatory cladocerans (Fig. 6). The assemblage of predatory cladocerans shifted from one with about equal contributions of *L. kindtii* and *B. longimanus* in the early summer to one completely dominated by *B. longimanus* in the fall.

As noted at the mid-depth site, the most separation in zooplankton among seasons at the offshore site was related to spring being well separated from all other seasons (Fig. 4). In contrast to the other two sites, where there was some separation between summer and fall, there was none at the offshore site; and instead, there was some separation in zooplankton assemblages between early and late summer. SIMPER indicated that Diaptomidae, *L. macrurus*, and *D. g. mendotae*, were each important to explain the dissimilarity between spring and other seasons along with *Cyclops* spp. (early summer and fall), *E. lacustris* (late summer) and *B. longimanus* (late summer and fall). Total biomass was lowest in the spring due to low biomass of each of these respective groups (Figs. 5, 6). The zooplankton assemblage was 99% copepods in the spring at the offshore site but only 82% (early summer), 63% (late summer) and 81% (fall) thereafter (Fig. 5). The continued contribution of cladocerans into the fall at the offshore site contrasts with their near complete disappearance at the nearshore and mid-depth sites. *B. longimanus* was the dominant predatory cladoceran in each season at the offshore site (Fig. 6). There was a large increase in *B. longimanus* biomass between early and late summer, and biomass remained high into the fall, when predatory cladocerans accounted for 5% of the total zooplankton biomass.

Chlorophyll *a* concentrations were highest at the nearshore site within each season, with highest concentrations in the spring or early summer. Chlorophyll *a* concentrations at the mid-depth and offshore sites varied little during the year. Water temperatures were highest at the nearshore site during spring and early summer, indicating an earlier warm up than at the deeper sites (Table 3).

Annual variation within sites

ANOSIM indicated that there was no difference among years at the nearshore site ($R = 0.01$, $p = 0.45$). By contrast, there were significant differences among years at the mid-depth site ($R = 0.20$, $p = 0.010$) and the offshore site ($R = 0.42$, $p = 0.001$). Although there were significant differences among years, the MDS plot indicated that zooplankton assemblages were not well separated for most sets of years at the mid-depth site (Fig. 4). For the offshore site, the main differences among years were generally related to zooplankton assemblages during 2007–2008 being separated from those in 2010–2012 (Fig. 4). At the offshore site, SIMPER indicated that the differences between 2007–2008 and 2010–2012 were related to increases in *D. g. mendotae* and *Cyclops* spp. and decreases in *L. macrurus* and *B. longimanus* in 2010–2012 (Fig. 7). Although Diaptomidae contributed to the dissimilarity between these sets of years, their overall abundance was generally unchanged or only changed slightly.

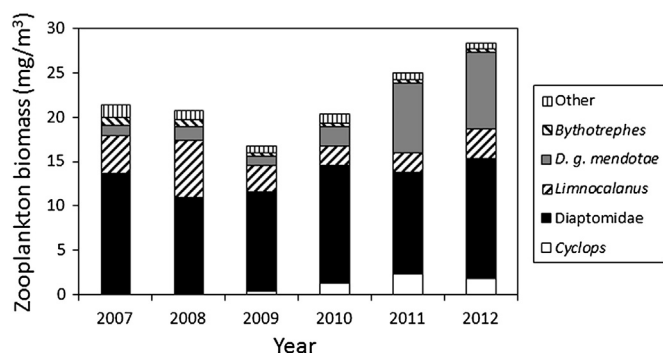


Fig. 7. Annual mean biomass concentration of zooplankton at an offshore site in southeastern Lake Michigan during 2007–2012.

Discussion

The dreissenid mussel expansion is not complete in the offshore regions of Lake Michigan (T. Nalepa, Univ. of Michigan, pers. comm) and our results were consistent with a system in transition. Somewhat contrary to expectations, there are still differences in the zooplankton assemblages between the nearshore, mid-depth and offshore regions in southeast Lake Michigan, but the differences depend somewhat upon season. There was little separation in zooplankton assemblages among sites in the spring and fall, but the nearshore site was generally well separated from the two deeper sites in the summer. This is consistent with results from Lake Michigan during 1973–1977 that found that the zooplankton community differences between the nearshore (4–10 m) and mid-depth region (30–45 m) intensified from spring into summer, but weakened in the fall (Evans, 1990).

One factor that contributed to the community assemblage differences among sites was variation in overall biomass of zooplankton. Total overall biomass was lower at the nearshore site relative to that at the mid-depth site, but overall biomass at the nearshore and offshore sites did not differ. Furthermore, although predatory cladoceran biomass was similar among sites, *B. longimanus* biomass remained highest in the offshore region and lowest in the nearshore region. This contrasts with our expectation that *B. longimanus* biomass would be similar between nearshore and offshore sites.

Comparing trends in biomass among sites to historical patterns is difficult because of limited historical data. Most data on zooplankton biomass in southeastern Lake Michigan is from depths <50-m and sampling at deeper sites (i.e., 100-m) was done mainly in the summer with samples taken in the top 40–50-m of the water column (Hawkins and Evans, 1979; Scavia et al., 1986). However, assuming that 90% of the zooplankton biomass was in the upper 40–50-m in the summer (S. Pothoven, unpublished data), we can convert upper water column volumetric biomass at the 100-m sites in the 1970s to whole water column biomass estimates comparable to our data. Thus, in the late 1970s, it appears that zooplankton biomass was highest in the mid-depth region (60 mg/m³), followed by the nearshore region (42 mg/m³), and lowest in the offshore region (29 mg/m³) (Hawkins and Evans, 1979; Scavia et al., 1986). By contrast, in 2007–2012, overall zooplankton biomass had converged between the nearshore (20 mg/m³) and offshore (22 mg/m³) regions. Although biomass at the mid-depth region (26 mg/m³) remained higher than at the nearshore/offshore sites, there appears to be a trend toward similarity in biomass between nearshore, mid-depth, and offshore regions. A more complete picture can be found from Lake Ontario where data from 1995 to 1997 indicated that zooplankton biomass concentration in the nearshore habitat (10 m deep) had become more similar to that at deeper sites (>20 m) following dreissenid invasion (Hall et al., 2003).

Because food (i.e., chlorophyll concentration) and water temperature are considered two of the most important factors controlling

zooplankton abundance (Palatas, 1972; Stockwell and Johannsson, 1997), we might have expected that biomass would be highest at the nearshore site, where mean water temperature and chlorophyll concentrations exceeded those found at the deeper sites. Instead, biomass concentrations of zooplankton between the nearshore and offshore regions were similar, highlighting the complexity of the relationship between food, water temperature, and zooplankton (see Palatas, 1972) and the need to consider other factors as well. For example, differences in predation pressure along the nearshore to offshore gradient are known to influence zooplankton communities in Lake Michigan (Makarewicz et al., 1995).

Another factor that contributed to spatial variation in zooplankton assemblages was differences in zooplankton composition among sites. One notable pattern was a higher percentage of large-bodied zooplankton groups in the offshore and mid-depth zones relative to the nearshore, a pattern that also existed in the past and was attributed to higher predation by fish on zooplankton in nearshore Lake Michigan (Evans and Jude, 1986; Evans, 1990; Pothoven et al., 2007). For example, the proportion of herbivorous cladoceran biomass comprised of the large bodied *D. g. mendotae* ranged from 23% (nearshore) to 77% (mid-depth) to 96% (offshore), with the small bodied *B. longirostris* accounting for nearly all of the remaining herbivorous cladoceran biomass at each site. Increases in *Daphnia* spp. relative to smaller cladocerans like *Bosmina* have been related to declines in planktivorous fishes in the Great Lakes (Wells, 1970; Pothoven et al., 2013) and smaller lakes (Brooks, 1968). The deeper water column in the offshore region provides a refuge from visually feeding vertebrate and invertebrate predators (Lampert, 1993; Pangle and Peacor, 2006) and thus indirectly contributes to the higher proportion of large bodied cladocerans compared to nearshore regions. Planktivores in the nearshore are more concentrated in a shallower water column with less chance for zooplankton to use vertical migration to find refuge from predators.

Larger copepods were found at the offshore sites as well. For example, there was a higher percentage of small bodied diaptomids (*L. minutus*) at the nearshore site compared to a higher percentage of large bodied diaptomids (*L. sicilis*) at the offshore and mid-depth sites. The percent contribution of the large bodied calanoid copepod *L. macrurus* also increased with depth of site. The prevalence of large calanoid copepods such as *D. sicilis* and *L. macrurus* in the mid-depth and offshore regions is not surprising because these species are usually found in the deeper, cooler regions of lakes (Balcer et al., 1984). Spatial and temporal variation in fish planktivory can also influence the abundance and spatial distribution of large copepods (Wells, 1970; Evans, 1990).

Differences in the predatory cladoceran assemblage also contributed to differences among sites. The small bodied *C. pengoi* was most abundant at the nearshore site and the large bodied *B. longimanus* was most abundant at the offshore site. Although fish abundance has declined in Lake Michigan, alewife *Alosa pseudoharengus* remain the most abundant fish planktivore in the lake. Alewife selectively consume the larger *B. longimanus* over *C. pengoi* (Pothoven et al., 2007; Storch et al., 2007) and can limit *B. longimanus* abundance in nearshore regions (Pothoven et al., 2007). Furthermore, even though fish numbers have declined, *B. longimanus* in Lake Michigan continue to have small broods and large neonates, adaptations attributed to help limit predation by gape-limited fish (Pothoven et al., 2012). The spatial separation between *B. longimanus* and *C. pengoi* could also reflect overlap with appropriate sized prey. Differences in optimal temperatures could also help explain spatial differences in the abundance of species such as *B. longimanus* (Cavaletto et al., 2010), as well as seasonal patterns, including their importance at all sites in the fall.

In addition to fish predation, predatory invertebrates, including the invasive *C. pengoi* and *B. longimanus*, can influence zooplankton assemblages (Laxson et al., 2003; Lehman and Cáceres, 1993). The impact of invasive predatory cladocerans was evident based on the rarity of *Daphnia retrocurva* and *Daphnia pulicaria* at all sites in this study. Historically, the small bodied *D. retrocurva* was an important component

of the *Daphnia* spp. assemblage in Lake Michigan (Evans and Jude, 1986). Furthermore, declines of alewife in the early 1980s led to an increase in the large bodied *D. pulicaria* in the offshore regions of Lake Michigan (Evans and Jude, 1986). Both *D. pulicaria* and *D. retrocurva* are quite vulnerable to predation by *B. longimanus* (Lehman and Cáceres, 1993; Schulz and Yurista, 1999) and *D. retrocurva* is also vulnerable to predation by *C. pengoi* (Laxson et al., 2003), and neither appears to have rebounded in abundance. Although *D. g. mendotae* are also vulnerable to *B. longimanus*, they are apparently able to persist in deeper regions, possibly due to behavioral modifications (Schulz and Yurista, 1999; Pangle and Peacor, 2006). However, these behavioral changes could lead to lower production of *D. g. mendotae* as they move into deeper, cooler water to avoid visual predators (Pangle and Peacor, 2006).

Despite declines of planktivorous fish to historical lows since the 1970s (Bunnell et al., 2014), zooplankton biomass in 2007–2012 had also declined around 24% relative to 1977 for the offshore (Scavia et al., 1986) and 52% and 57% relative to 1975–1976 for the nearshore and mid-depth regions, respectively (Hawkins and Evans, 1979). The fact that zooplankton biomass did not increase following declines in fish planktivores suggests that the oligotrophication taking place in Lake Michigan following dreissenid invasion and proliferation (Evans et al., 2011; Fahnenstiel et al., 2010; Pothoven and Fahnenstiel, 2013) could be affecting zooplankton production. The declines in zooplankton biomass are consistent with other studies that have found zooplankton declines of similar magnitude following dreissenid invasions (Higgins, 2014; Kissman et al., 2010). If primary production in the nearshore and offshore regions continue to become more similar (Fahnenstiel et al., 2010; Schelske et al., 1980), the capacity for the nearshore zooplankton assemblages to sustain higher relative levels of fish predation will likely be diminished. However, considering that dreissenid mussel's impact in the nearshore region goes back to the late 1990s and mussel biomass there appears to be stabilizing, perhaps mussel impacts in the nearshore region have been more or less realized and nearshore zooplankton biomass will remain stable. On the other hand, offshore zooplankton biomass could continue to decline as direct mussel impacts are only beginning to be realized in this region.

Another explanation for the absence of a positive response of zooplankton biomass to fish declines is that declines in fish planktivores led to an increase in the abundance of invertebrates such as *B. longimanus*, which became a dominant planktivore in Lake Huron following declines in fish (Bunnell et al., 2011; Pothoven and Höök, 2014). However, other than relatively high biomass in 2007–2008, the mean biomass of *B. longimanus* in the offshore region during 2009–2012 (0.37 mg/m^3) was fairly similar to 1994–2003 (0.30 mg/m^3 ; Vanderploeg et al., 2012). Nonetheless, the relative impact of *B. longimanus*, particularly in the offshore, may have increased in recent years because they now account for a higher proportion of the zooplankton biomass and increased light penetration has likely improved their predatory success rates (Vanderploeg et al., 2012).

Seasonal zooplankton differences continue to be an important attribute of both nearshore and offshore communities. For example, seasonal patterns in zooplankton assemblages varied among sites and may have been related in part to biological responses to the progression of warming temperatures from nearshore to offshore. Cladoceran appearance each year is related to water temperature (Balcer et al., 1984), and the nearshore region has a pulse of warm water (as well as chlorophyll) in the spring before the other sites. Other studies in the Great Lakes have found that an inshore pulse of zooplankton preceded that in the offshore habitat owing to more rapid warming in the nearshore habitat (Carter and Watson, 1977; Watson and Wilson, 1978). This is consistent with our observation that peak biomass in the nearshore region was in early summer, whereas at the mid-depth and offshore sites, peak biomasses were found in late summer. Zooplankton abundance during early summer can be a critical factor that determines recruitment success of some nearshore fish such as yellow perch *Perca flavescens* in Lake Michigan (Dettmers et al., 2003).

In addition to seasonal variation within a site, we noted annual variation, especially at the offshore site, with the zooplankton assemblage during 2007–2008 differing from that found in 2010–2012. These differences were due largely to increases in *D. g. mendotae* and *Cyclops* and decreases in *B. longimanus* and *L. macrurus* in 2010–2012. Although increases of *D. g. mendotae* could indicate declining fish predation pressure, this idea is not consistent with declining *L. macrurus* biomass (Evans, 1990; Wells, 1970). Increased biomass of *D. g. mendotae* and *Cyclops* could be related to the declines of *B. longimanus*, which eat *D. g. mendotae* and *Cyclops* nauplii (Schulz and Yurista, 1999). However, the declines in *B. longimanus* were somewhat curious, considering that would be inconsistent with declining fish numbers. Perhaps *B. longimanus* in 2007–2008 experienced an initial increase in biomass following fish declines (see Vanderploeg et al., 2012) that could not be sustained due to a prey base that was potentially limiting even prior to oligotrophication in the offshore (see Lehman and Cáceres, 1993; Burkhardt and Lehman, 1994; Yurista et al., 2010). The changes in the zooplankton assemblage at the offshore site do not appear to be related to water temperature because two of the years that clustered together had the highest (2012) and lowest (2011) annual temperatures of the time series. Increases in cladocerans and cyclopoid copepods can reflect a shift toward a more productive environment (Gannon and Stemberger, 1978), but this does not appear to have occurred either because annual chlorophyll *a* levels only ranged between 0.9 and 1.1 $\mu\text{g/L}$ for 2007–2012 at the offshore site. Thus, there appeared to be a shift in the zooplankton community at the offshore site, but the reasons for the shift appear to be unclear and merit further investigation.

By contrast to the offshore and mid-depth sites, there were no differences among years at the nearshore site, which was characterized by more variation within years than between years. The nearshore region is in close proximity to anthropogenic disturbances and is less stable than the offshore regions (Yurista et al., 2005, 2006, 2009). The nearshore region is subject to variable influences such as upwelling, wind events, and river plume dynamics that would have much less influence on the deeper offshore regions. Thus, detecting inter-annual changes in the zooplankton assemblage at a nearshore site is likely more difficult than at offshore sites owing to the variability encountered in the nearshore.

This study provides evidence for the dynamic nature of the zooplankton community in Lake Michigan that is influenced by many traditional factors (vertebrate and invertebrate predation, temperature, phytoplankton) and new ones (dreissenid mussels). As the lake becomes more oligotrophic, zooplankton biomass appears to have declined at all the depth regions examined, with biomass converging between the nearshore and offshore stations. Nevertheless, there are still differences in the composition of the zooplankton communities between the nearshore and offshore regions that may be related to factors such as differences in predatory cladoceran composition, potential differences in fish predation pressures, and the availability of deepwater refuges. Because the dreissenid populations is still expanding in the offshore regions, the clear role of oligotrophication may not be evident for some time yet as the offshore region remains in a transitional state.

Acknowledgments

We would like to thank all those involved in data collection and analysis, in particular the crews of the RV *Shenelon* and RV *Laurentian*, D. Ruberg, A. Sookhai, A. Zantello, and J. Elliot. GLERL contribution number 1732 and MTU contribution 18.

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